



Impacts of Climate Change on Terrestrial Ecosystem Functioning – An Overview

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IMPACTS OF CLIMATE CHANGE ON TERRESTRIAL ECOSYSTEM FUNCTIONING

- An overview



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Cover photo: The layout of the experimental site at Brandbjerg showing 12 octagons in 2 groups. ©Kim Pilegaard.

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IMPACTS OF CLIMATE CHANGE ON TERRESTRIAL ECOSYSTEM FUNCTIONING

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Collaborators:

The CLiMA!TE project was carried out during the years 2004-2015 in a collaboration between the Risø National Laboratory (now Technical University of Denmark), the Royal Veterinary and Agricultural University (now University of Copenhagen), the National Environmental Research Institute (now Aarhus University), and University of Copenhagen.

Thank you to:

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CLiMA!TE main findings:

Plants

- THE PLANT COMMUNITY INCREASED PHOTOSYNTHESIS WITH ABOUT 35% in response to elevated CO₂. Despite the high assimilation of carbon, the aboveground vegetation did not increase growth whereas we saw a consistent increase in root biomass especially in the deeper roots with elevated CO₂.
- PHOTOSYNTHESIS WAS DOWN-REGULATED DURING DROUGHT EVENTS in *Calluna vulgaris* plants followed by recovery after re-wetting. This indicated an extreme resistance to drought by down-regulation of productivity in periods with water limitation. In contrast, *Deschampsia flexuosa* has a high resilience to changes in climatic factors determined by its capability for rapid dieback and regrowth.
- THE PLANTS INITIATED SPRING GROWTH ABOUT 2 WEEKS EARLIER WITH WARMER TEMPERATURES . However, the larger spring growth did not translate into higher peak biomass in summer probably due to a slight decrease in soil water content with higher temperature.
- OVERALL, WE OBSERVED SMALL RESPONSES IN THE VEGETATION TO THE CLIMATIC CHANGE showing high resilience or resistance. However, after extreme events where plants have to regenerate, we observed high sensitivity to even moderate climate change with potential shift from heathland to dry grassland.

Microorganisms and soil fauna

- SOIL BACTERIAL RESPONSES TO CLIMATE CHANGE WERE MODEST and limited to increases in bacterial activity and abundance by warming. Soil and root-associated fungi showed more profound changes.
- ELEVATED CO₂ LED TO INCREASED COLONIZATION BY ARBUSCULAR MYCORRHIZAL FUNGI, which alleviated the increasing plant nitrogen demand in consistence with higher root growth and plant nutrient demand. Soil animals such as nematodes predominantly feeding in the rhizosphere benefited from the increase in food sources under elevated CO₂. Enchytraeids were also stimulated by CO₂ in the early part of the experiment, but this effect was not observed after 7-8 years of treatments.
- DROUGHT SEEMED TO STIMULATE FUNGAL ACTIVITY AND ABUNDANCE with no change in community composition, suggesting a high degree of fungal adaptation to dry conditions. Likewise, soil mites seemed unaffected by drought while enchytraeids, Collembola and nematodes were only transiently reduced by drought and seemed to recover quickly after re-wetting. Hence, soil biota in this ecosystem type seemed well adapted to recurrent drought episodes.
- OVERALL, SOIL FAUNA BIODIVERSITY AND ABUNDANCE WAS LITTLE INFLUENCED, if at all, by the full combination of warming, increased drought and CO₂.

Soil

- FLUX MAGNITUDES OF NON-CO₂ GREENHOUSE GASES CH₄ AND N₂O WERE GENERALLY SMALL. In the future soil oxidation of CH₄ may increase, whereas soil-atmosphere exchange of N₂O remains unaltered.
- SOIL RESPIRATION INCREASED PERSISTENTLY BY ELEVATED CO₂. Model predictions suggest that associated C losses would increase by ca. 21% in the future. Therefore, simultaneous stimulation of C assimilation and storage in plant biomass and litter must be in excess of 21% for this ecosystem to not suffer a reduction in net ecosystem exchange.
- BOTH THE LABILE 3% AS WELL AS THE BULK POOL OF SOC REMAINED UNCHANGED under the simulated future conditions suggesting that top SOC may provide a persistent buffer in the overall C-cycle. The majority 97% of the soil organic carbon (SOC) in the top soil was characterized as recalcitrant carbon with a mean residence time of 100-150 yrs..

Nitrogen and carbon turnover

- SLOWER SHORT-TERM N TURNOVER IN THE FULL TREATMENT INDICATED A RESTRICTION OF THE POTENTIAL GROWTH RESPONSE OF PLANTS TO ELEVATED ATMOSPHERIC CO₂ CONCENTRATION IN THE FUTURE. The decreased N turnover was caused by lower mineralization rates below ground in response to drought. In addition, increased C/N ratios of the photosynthetic tissue caused by elevated CO₂ indicated lower litter quality in the future.
- RESPONSES WERE SMALLER IN COMBINED TREATMENTS THAN IN SINGLE TREATMENTS. Interactions between treatments were common and although some synergistic effects were observed, antagonism dominated the interactive responses in treatment combinations.
- PRELIMINARY RESULTS INDICATE THAT THE FULL COMBINATION OF TREATMENT FACTORS REDUCED THE NET C UPTAKE BY MORE THAN 50%, whereas exposure to each of the single factors led to increased net C uptake. This demonstrates important interactive effects among the climate change factors with major implications for ecosystem C feedback under future climate.

Perspectives

- WE NEED NEW EXPERIMENTS ADDRESSING EXTREME EVENTS, TIPPING POINTS AND THRESHOLDS. Current climate change experiments have often focused on predicted "average" changes while climate extremes and especially really severe extremes are less well covered.
- NEW EXPERIMENTS ARE NEEDED TO ADDRESS MULTIPLE LEVELS OF TREATMENTS. Most experiments have focused on one level of a given treatment compared to an untreated reference. New experiments need to address response surfaces with several levels of each treatment instead of single level response. This will also support more focus on thresholds and tipping points.
- ECOSYSTEM EXPERIMENTS NEED TO BE STRONGLY INTEGRATED WITH ECOSYSTEM MODELS, especially when studying impacts of climate extremes.

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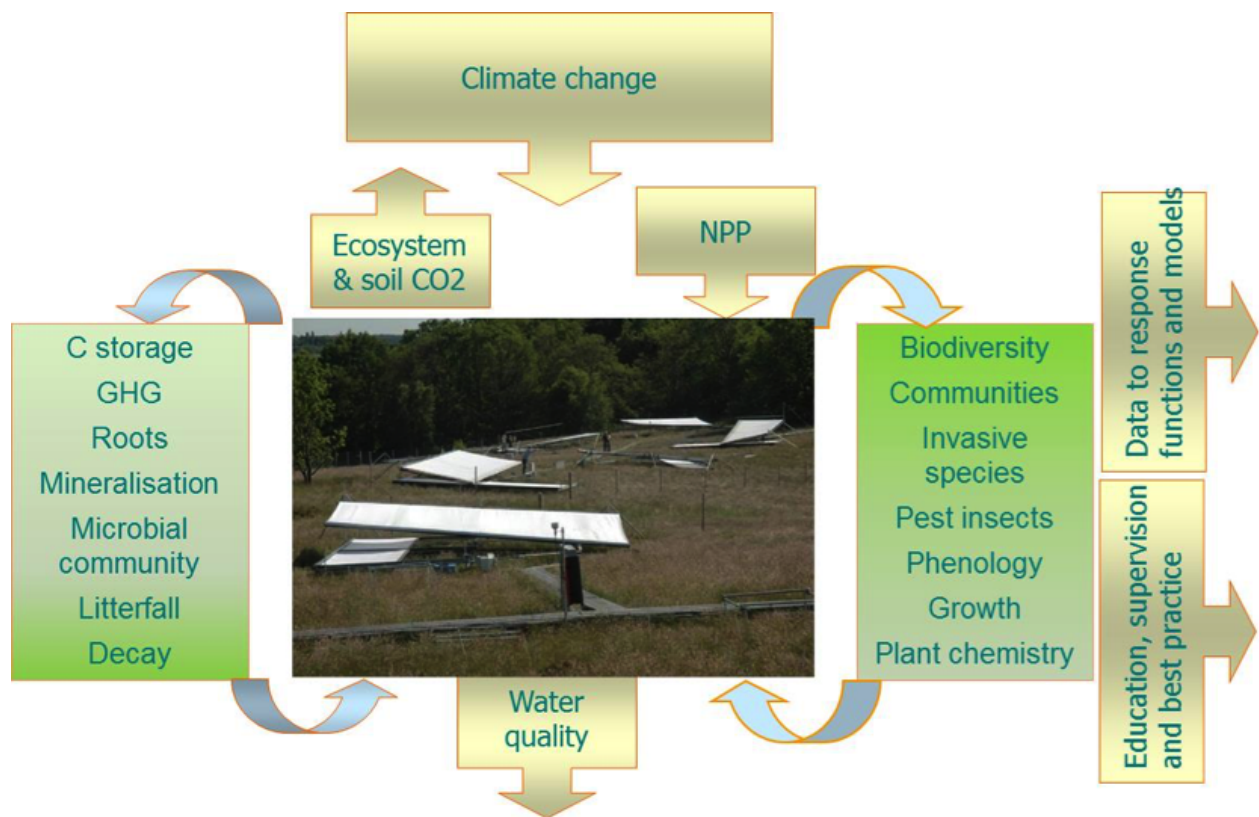


Figure 1: Conceptual overview of the CLiMA!TE project. ©Inger Kappel Schmidt.

Introduction

CLiMA!TE - background

The concentration of CO₂ in the atmosphere is increasing, global temperatures are increasing, and local precipitation patterns are changing with increases in the intensity of rain events and drought periods. This is expected to affect the structure and functioning of terrestrial ecosystems (IPCC, 2013) with major impacts on natural environments as well as ecosystems used for agriculture or forestry. Over the past three decades, major efforts have been devoted to understand and predict such impacts of climate change on ecosystem processes and functioning in order to understand the urgency of the changes as well as the possibilities for ecosystem adaptation or climate change mitigation. These efforts have included observations of past changes, monitoring of ongoing changes, observations across environmental gradients (space for time substitution), ecosystem manipulation experiments mimicking future climate changes, and dynamic ecosystem modelling (Beier, 2004; Rustad, 2008). Each of these approaches has their forces and drawbacks, but across all a general limitation is that observations and experiments have focused on one single climate factor. For example, observations across gradients can hardly combine simultaneous and ideal differences in two or even three climate factors at the same time to provide a multi factor response picture. Ecosystem experiments, which could do it, often limits themselves to one factor for practical reasons or because of lack of resources, since inclusion of one extra factor doubles the number of experimental units and the demand for resources in a classic experimental design. Therefore, very few multi factor climate change experiments exist. Instead the underlying assumption has been that if the individual responses are known based on single factor experiments, then dynamic ecosystem or global models can predict the responses of the combined factors. This approach may seem reasonable but is constrained by at least two problems, which CLiMA!TE specifically aimed to overcome:

1. When several factors act together, they may interact, and these interactions among the different climate change factors may not be linear and/or predictable. Computer models may predict some of these interactions relatively well (e.g. resource limitations due to increased growth), while other interactions may be unpredictable.

The assumption that the impact of the "climate change cocktail" may be predicted from an understanding of the individual factors may therefore be erroneous.

2. Even when models do predict the interactions, we still need multi factor experiments to train and test the models in order to know if the predictions are correct.

Another inherent problem related to climate change and experimentation is the time scale. Climate change acts over decades, meaning that climate change experiments running for 2-4 years only highlight short term and transient effects on the ecosystems, while lacking the ability to inform about long term and more stable effects. The "long term" perspective of climate change was therefore another important rationale for the CLiMA!TE experiment.

The "long term" perspective of climate change calls for long term experiments, which for decades has been argued from the scientific community, was therefore another important rationale for the CLiMA!TE experiment. The VILLUM FOUNDATION provided a very rare opportunity to pursue this in reality.

In summary, the CLiMA!TE experiment was driven by two major rationales: 1) a need for realistic experiments involving combinations of the main climate change drivers and 2) the long term perspective of climate change.

CLiMA!TE - the multi factor approach

The aim of CLiMA!TE was to establish an experiment mimicking a "realistic" climate scenario for Denmark by year 2075 with focus on the three main factors involved in climate change (CO₂, temperature and drought). The intention was to run the experiment for up to ten years with "state of the art" experimental designs technically as well as statistically. The ten year time perspective lead to a decision that the annual "drought" treatment needed to be moderate in the sense that we did not want to "kill" the plants (or even the ecosystem) as this would compromise the long term perspective. This has consequences for the interpretation of the results, which will be discussed later. The combined technical and statistical design involved six replicates of each treatment to provide enough statistical power needed considering the large spatial variability, and a split-plot design, making the large number of plots (n=48) manageable from a practical and resource point of view. Each treatment factor was applied at one level (2075 forecast) and compared with the ambient level which again, has consequences for interpretation of the results, which will be discussed later.

Experimental design

The CLiMA!TE experiment was designed to match the climate scenario for Denmark in year 2075 as closely as possible, with elevated CO₂ at 510 ppm, elevated temperature of ca 2°C and extended summer droughts, although the predicted scenario includes incidents of more heavy summer and winter rainfalls but with only small changes in annual rainfall (<http://www.dmi.dk>). The experiment includes plots with elevated CO₂ concentration (CO₂), elevated temperature (T), induced drought in late spring/summer (D) and untreated controls for reference (A). The treatments are combined in all combinations (A, T, D, CO₂, TD, TCO₂, DCO₂, TDCO₂). The eight treatments are placed in pairwise octagons of 6.8 m across receiving ambient and elevated CO₂, respectively. Each octagon is divided into four "slices" (9.1 m² per plot) to provide all eight treatment combinations (Figure 2). Each combination is replicated six times, (total of 48 plots) in a split-plot design with six octagons at ambient CO₂ and six receiving elevated CO₂. The distances between the octagons are at least 2.5 times the octagon widths to avoid CO₂ contamination from the elevated to the ambient CO₂ octagons. Board walks connect the octagons to avoid disturbance by trampling between the plots and a flexible board walk system in each octagon provides easy access and prevents trampling within the plots.

Free Air Carbon Enrichment (FACE) – CO₂ treatment

The CO₂ is distributed by a FACE system (Miglietta et al. 2001) where pure CO₂ is distributed from a central CO₂ tank to six CO₂-elevated octagons, each of which has computer controlled CO₂ concentration at 510 ppm. The CO₂ control is dynamic in relation to changes in [CO₂] monitored at the centre of the plot (30 cm height); wind speed and wind direction is measured by a 2D-anemometer placed outside the octagon in 2 m height. The CO₂ fumigation starts 30 min after sunrise and ends 30 min before sunset all year round, except during periods with full snow cover of the vegetation. The amount of CO₂ injected is varied by increasing/decreasing the gas pressure in the pipes by means of automatic pressure regulators.

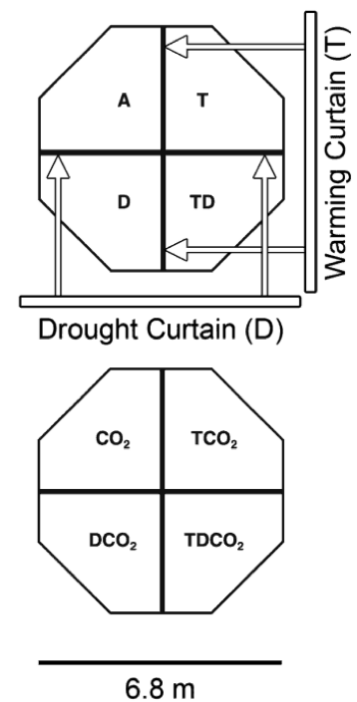


Figure 2: Schematic presentation of a block with two separate octagons receiving elevated CO₂ and ambient CO₂, respectively, and together hosting all eight treatment combinations with CO₂ (CO₂), warming (T), drought (D) and untreated control (A). Curtains are only shown on the ambient CO₂ octagon. Modified from Mikkelsen et al. 2008.

Temperature enhancement

The temperature enhancement is conducted as "passive night-time warming" (Beier et al. 2004). The warming plots are covered by a light scaffolding (h = 0.5 m) carrying a curtain that absorbs and re-emits infra-red radiation (Bruhn et al. 2013). The curtains are coiled on a beam and automatically operated by an electronic controller according to pre-set conditions during the whole year: Day/night - curtains are pulled over the vegetation at sunset and retracted at sunrise; Rain - curtains are retracted in case of rain during the night (sensitivity < 0.1 mm); Wind - the curtains are removed at high winds (> 7 m s⁻¹); and Dew fall - the curtains are removed in case of dew fall (max 30 min.) spring/summer precipitation.



Figure 3: Clearly visible effect of passive night-time warming on a winter morning. ©Poul Therkild Sørensen.

Drought treatment

The drought treatment is constructed similar to the warming treatment, except that the curtains are controlled by a rain sensor activating the curtains to cover the plots whenever it rains and to remove the curtains when the rain stops. The curtains are removed automatically if the wind speed exceeds 7 m s⁻¹. The drought treatments were normally stopped after ca 5 weeks or when the soil water content reached ca 5 vol % water content in the top 20 cm of the soil, which is slightly above the wilting point of the vegetation at the site.

Experimental control measurements

Within each experimental octagon or plot, parameters are monitored to check the treatments and their effects on the physical and climatic conditions. Temperature is measured in the vegetation canopy (+20

cm), the top soil (0 – 2 cm) and the soil (–5 cm) in each treatment plot every minute and averaged over 10-min intervals. Soil moisture is measured by TDR at 0–60 and 0–20 cm soil depths providing half-hourly averages. The CO₂ concentration is measured sequentially in all octagons and at two positions 30 m away from the nearest FACE octagon. The air is sampled continuously at the centre of each octagon through a $\varnothing 3$ mm PVC tube, connected to a vacuum pump and a CO₂ monitor to provide measurements of [CO₂] of each octagon every 40 min.

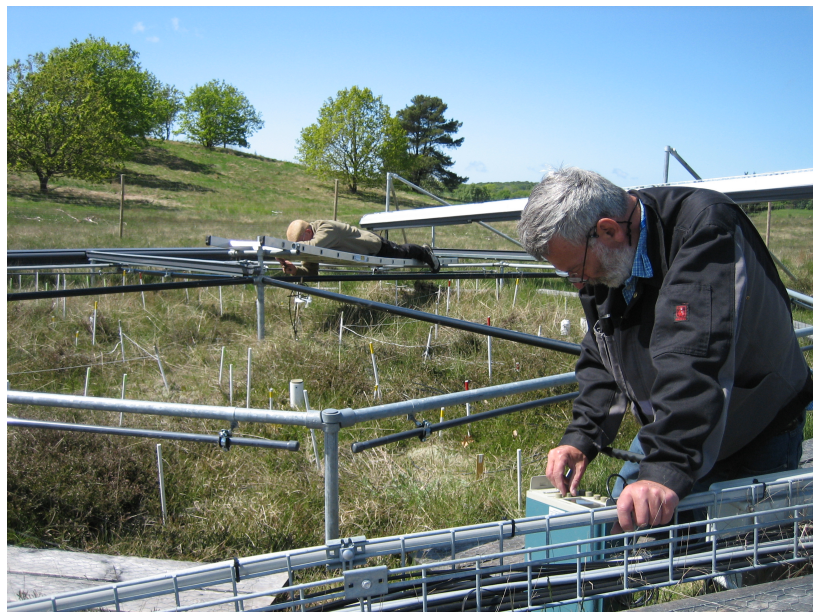


Figure 4: Maintenance of soil sensors in treatment plot. ©Teis N. Mikkelsen.

Weather conditions

Two independent weather stations situated within the experimental area and 75 m apart collect basic meteorological data at 2 m height, including: photosynthetic active radiation (PAR), relative humidity (RH), temperature and precipitation.

For further details on the experiment and experimental set-up see Mikkelsen et al. (2008).



Figure 5: Heather (*Calluna vulgaris*).
©Teis N. Mikkelsen.

Impacts on plants

Plant communities



Figure 6: Aerial photograph of one of the octagons of the CLiMA!TE experiment where the dark green purple areas represent *C. vulgaris* bushes and the green/brown areas represent *D. flexuosa*. Growth and competition were followed by aerial photos, NDVI, pinpoint and leaf level measurements of photosynthesis. ©Johannes Ransijn.

The plant community showed high resilience to changes in climate. The community was dominated by the grass *Deschampsia flexuosa* (wavy hairgrass) and the evergreen dwarf shrub *Calluna vulgaris* (heather). The grass *D. flexuosa* is expected to be more flexible and opportunistic in its responses to climatic change than *C. vulgaris*, an evergreen sclerophyllous dwarf shrub. We studied both the competition and the growth strategies in the two species under climate change (Albert et al. 2011; Damgaard et al. 2009; Ransijn et al. submitted).

D. flexuosa down-regulated photosynthetic capacity under elevated CO₂ and was flexible in its adjustment of leaf level photosynthetic capacity dependent on water availability. *D. flexuosa* could opportunistically green up earlier in warmer springs and flexibly re-

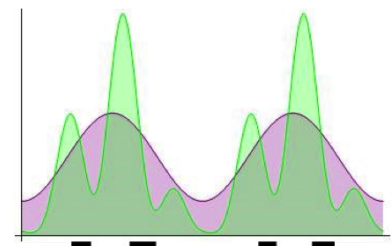


Figure 7: Typical responses to stress events (black lines) of a low flexibility species (purple; *C. vulgaris*) and of an opportunistic species (green; *D. flexuosa*)

duced its green biomass under drought conditions. This reduction was followed by quick recovery during re-wetting. *C. vulgaris* did not show profound down-regulation of leaf level photosynthetic capacity under elevated CO₂ (Albert et al. 2011b; Ransijn et al. submitted). *C. vulgaris* was less flexible than *D. flexuosa* at all levels and hardly adjusted green biomass to drought or warming.

In general, the plants responded to the climate manipulations as we hypothesized. In the plots subjected to night-time warming, the plants initiated growth two weeks earlier resulting in increased spring biomass (Kongstad et al. 2012; Ransijn et al. submitted). In the warmed plots, the water content in the soil was reduced due to both the treatment and increased water uptake by a larger biomass and we did not observe any effects of increased temperature. Drought was applied each year in spring during maximal growth and reduced plant biomass by about 20 %. However, quickly after re-wetting of the soil, the plants recovered fully and the drought had no significant effect on annual aboveground biomass production. Elevated CO₂ stimulated the assimilation of carbon, but did not influence the aboveground biomass for either *D. flexuosa* or the ecosystem as more litter was produced. However, root biomass and production increased in elevated CO₂ in several years and more roots were found with depth under elevated CO₂ (Arndal et al. 2012; 2014; submitted), which may change plant communities in the future. We further observed an increased number of flowering culms in plots exposed to elevated CO₂ in two out of the five years. This indicated higher allocation to reproductive tissue (Kongstad et al. submitted).

Treatment combinations showed little interaction with the plant parameters, and in particular elevated CO₂ did not counterbalance the drought effect on plant growth, as we had anticipated. Inter-annual variability in climatic conditions affected both species in a similar way and did not alter the competitive balance between the species (Ransijn et al. 2015). We conclude that the two heathland species, on a short time scale, will be relatively resistant to the changes in climatic conditions. The high resilience in plant communities has been confirmed by other studies. It has been argued that the lack of responses is due to the small mean annual change in climate and that extreme events are needed to push the ecosystem as also demonstrated in a meta-analysis across European shrub-lands (Kröel-Dulay et al. submitted).

However, in contrast to these results are results from another climate experiment included in CLiMA!TE. At Mols, a more simple climate manipulation experiment with warming and drought as the only treatments was initiated in 1998. After only two years of climate treatments, a heather beetle (*Lochmea suturalis*) outbreak killed all the heather plants. The herbivory by the beetles was more severe in both the drought (Figure 8) and the warming treatment and during regeneration of *C. vulgaris* there was a much stronger effect of particularly the drought treatment on seedling survival resulting in a shift from heathland to grassland (Schmidt et al. submitted). Ma-

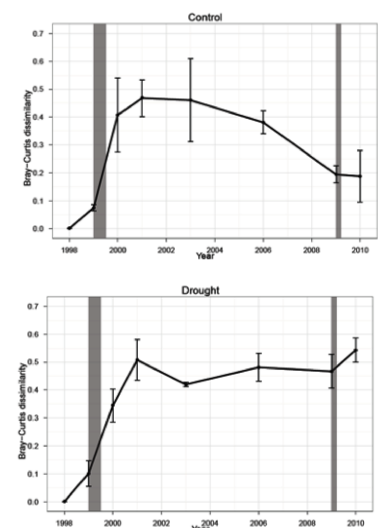


Figure 8: The Bray-Curtis dissimilarity between 1998 and 2010 vegetation community (mean \pm SE). The *C. vulgaris* plants were defoliated and killed by heather beetles in 1999.

ture plants may be more resilient than juvenile plants and climatic changes that had limited effect on mature plant communities may severely affect regeneration. One of the reasons for the higher susceptibility to climate change during regeneration may be the high shoot to root ratio in seedlings which off-set the resilience.

The results have implications for the design of future climate change experiments. It demonstrates the need for including extreme weather events or other disturbances, which set back the plants to the most sensitive phase in the plant life cycle with germination and establishment (Schmidt et al. in prep).

Leaf eco-physiology response to climate change

In general, our results show that elevated CO₂ stimulates net photosynthesis (P_n) in both *C. vulgaris* and *D. flexuosa*, and after some exposure time (months) a down regulation in potential photosynthesis (V_{cmax}) and a lower leaf nitrogen concentration was seen. This means that P_n is higher when the plants are exposed to elevated CO₂ compared to current ambient CO₂ (Figure 9) (Albert et al., 2011b; Albert et al., 2011c). Drought generally inhibited net photosynthesis (Albert et al., 2011a; Albert et al., 2011b) and increased temperature stimulated the photosynthesis in spring indirectly by affecting the soil temperature and thereby increasing the water and nutrient availability (Albert et al., 2011c). Plants also react directly to ambient temperature fluctuations and the P_n acclimation varied with a factor of 3-4 throughout the year for *C. vulgaris* and *D. flexuosa*, and was highest during the summer and lowest in the winter (Boesgaard, 2013), but the temperature treatment effects here are minor compared to the natural variation.

Surprisingly, no general reduction in stomatal conductance was seen in elevated CO₂ for *C. vulgaris* although this is often reported for other species. This suggests that the improved water use efficiency observed in our elevated CO₂ plots was caused by increased photosynthesis (Albert et al., 2011c).

When treatments are combined, the responses are getting more realistic since all three factors will change in the future climate, but interpretations will also be more complicated since fundamental plant physiological processes are affected in a way that is not predictable from single factor treatments (Albert et al., 2011b; Albert et al., 2011c).

The results above are reflecting the work done after 1-2 years of treatment, but after 6 years of treatment the eco-physiological responses are more or less similar (Boesgaard et al., 2013b; Boesgaard et al., 2013c). This means that the plants have acclimatized to the treatments in the beginning of the experiment, and afterwards kept this acclimatization at the same level. The quality of the gas exchange measurements was slightly improved (in the after 6 years campaign) by introducing a new technique, the leaf adaptor frame (LAF) (Boesgaard et al., 2013a).

A major frost episode occurring in the winter of 2010/11, caused

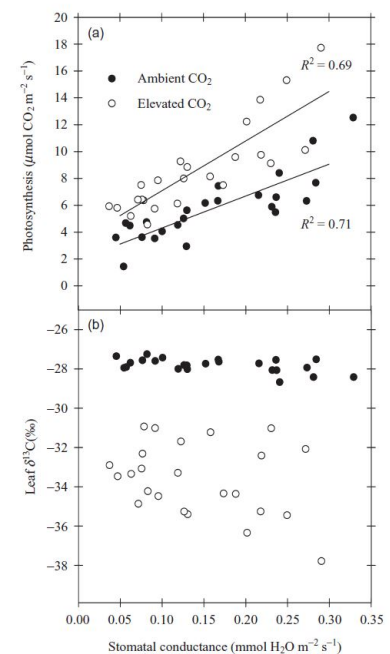


Figure 9: The relationship between stomatal conductance, net photosynthesis and leaf $\delta^{13}\text{C}$. Shown are the (a) average net photosynthesis versus average stomatal conductance, and (b) leaf $\delta^{13}\text{C}$ versus average stomatal conductance from each gas exchange campaign. From Albert et al., 2011c.

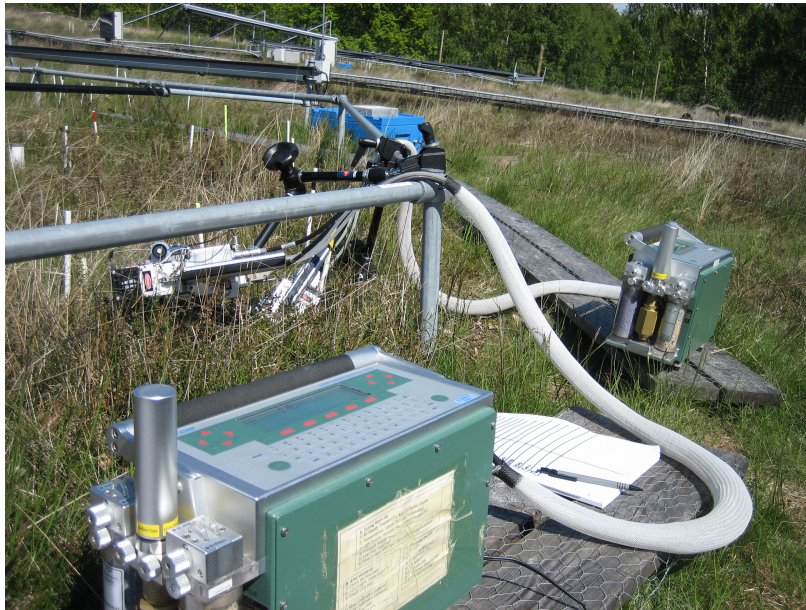


Figure 10: Leaf gas exchange measurement equipment in action. ©Teis N. Mikkelsen.

a major die-back of the standing population of *C. vulgaris* shoots. New shoots regrew from the root system with an approximate 75% regrowth, and the new shoots were then measured. In the beginning, in the warm season, no down-regulation of the photosynthetic capacity under elevated CO_2 was measured, but in the following autumn/winter (cold season) a down-regulation of photosynthetic capacity was observed. However, in both seasons the stimulation of photosynthesis was maintained in elevated CO_2 . No effect of warming was found in either of the seasons, but drought was found to counterbalance the CO_2 -induced stimulation of photosynthesis during warm season (Boesgaard et al., 2013b).

Plant strategies are important for interpretation of the eco-physiology responses and *C. vulgaris* and *D. flexuosa* have different strategies as exemplified here: During natural drought we detected that *D. flexuosa* responded with a combination of die-back of aboveground biomass and reduction of stomatal conductance during dry conditions, the grass continued to have high carbon uptake in the remaining leaves. The dwarf shrub *C. vulgaris* endured the dry conditions by preserving shoot biomass and reducing stomatal conductance (Albert et al., 2012). These different strategies may have a considerable impact on carbon uptake and on the ability of a species to compete, as future climatic changes are likely to extend the summer drought period together with the more frequent and extensive precipitation events outside the summer season (Albert et al., 2012).

Interaction with other factors than treatments factors can alter the outcome. In the autumn the Photosystem II (PSII) performance responses to low temperature were probed with chlorophyll-a fluorescence technique. Decreasing temperature during autumn linearly reduced $\text{PI}_{\text{total}}^1$, both in *D. flexuosa*, and in *C. vulgaris*, and following freezing events the PI_{total} and F_v/F_m ² were reduced even more.

¹ PI_{total} : the total photosynthetic performance.

² F_v/F_m : the maximal quantum yield of primary photochemistry in darkness.

In combinations with elevated CO_2 , interactive effects with drought, $\text{D} \times \text{CO}_2$ and warming, $\text{T} \times \text{D} \times \text{CO}_2$ were negatively skewed and caused the reduction of PSII performance in both species after occurrence of freezing events (Albert et al., 2013). The air pollutant ozone will also be a part of the future global change and it is phytotoxic. In a study where we exposed some of the long term treated CLiMA!TE plants with free air ozone, we showed that ozone become more toxic to photosynthesis processes when plants are acclimated to long term elevated CO_2 and drought (Albert et al., 2014).

Effects of elevated CO_2 , warming, and drought episodes on plant leaf eco-physiology vary with plant development, environmental conditions, and treatment load. These parameters have a seasonal and inter-annual variation and in combination with interacting eco-physiological responses some effects become temporal and transient while others are lasting. (Albert et al., 2011a; Albert et al., 2011b; Albert et al., 2011c; Albert et al., 2012; Albert et al., 2013; Boesgaard et al., 2013b; Boesgaard et al., 2013c).

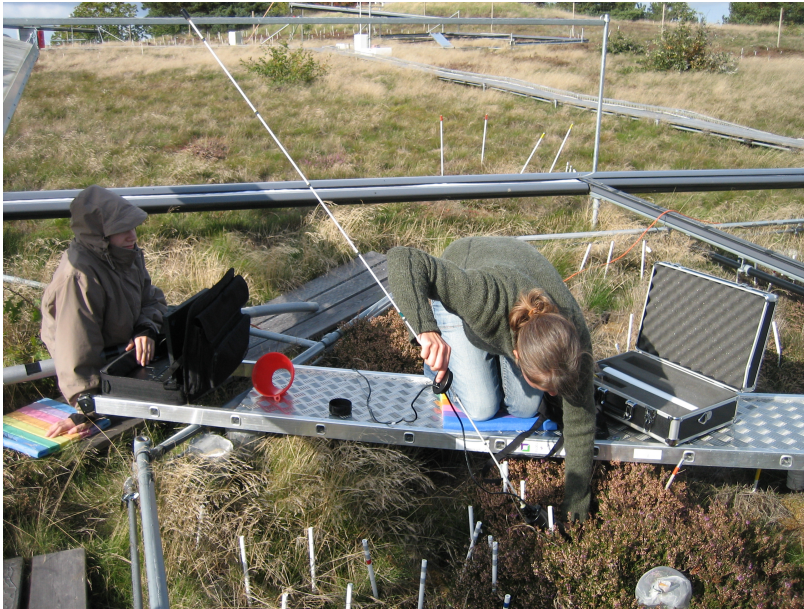


Figure 11: Investigation of root growth by rhizotrons. ©Teis N. Mikkelsen

Fine root response to climate change

The effects of climate change on roots are difficult to predict (Eisenstat et al., 2000). Climate change may affect a number of root parameters, as for example root biomass, which is important when determining the vegetation carbon stocks, and the root production and turnover, which determines the flux of C to the soil through C and N cycling. Also root length might be affected, which is important when determining the capacity for nutrient uptake. In light of climate change and ongoing debate on C sequestration by the vegetation, the role of roots have become increasingly important. It has been suggested that a large proportion of the additional carbon is

being sequestered in the terrestrial vegetation, and much of that is stored below ground (Gifford et al., 1996). Thus carbon cycling and the ability to sequester C will be driven more by below-ground than aboveground processes.

In the CLiMA!TE experiment, the main findings of the fine root responses to the treatment within the first 5 years were mainly due to elevated CO₂. The root biomass and production increased in elevated CO₂ in several years, and also the root length and root numbers increased. The distribution of roots also changed with depth under elevated CO₂, by increasing the number and roots length going deeper into the soil profile, as a way to search for more nutrients (Figure 12) (Arndal, in review). The fine root nitrogen concentration was often lower in elevated CO₂ in both *C. vulgaris* and *D. flexuosa* (Arndal et al., 2014; Arndal et al., 2013). As a way to alleviate nutrient limitation *D. flexuosa* roots increased their nutrient uptake of ammonium and its mycorrhizal colonization (Arndal et al., 2013). *C. vulgaris* did neither increase its nutrient uptake nor its mycorrhizal colonization, but increased the fine root production under elevated CO₂. Warming alleviated P limitation in *C. vulgaris* and both species increased the nitrogen and phosphorous pool in a future climate (Arndal et al., 2013). In a future climate we therefore might expect increased C storage in below-ground plant biomass, as the turnover was not affected by elevated CO₂, and changes in rooting depth might also affect the carbon fluxes.

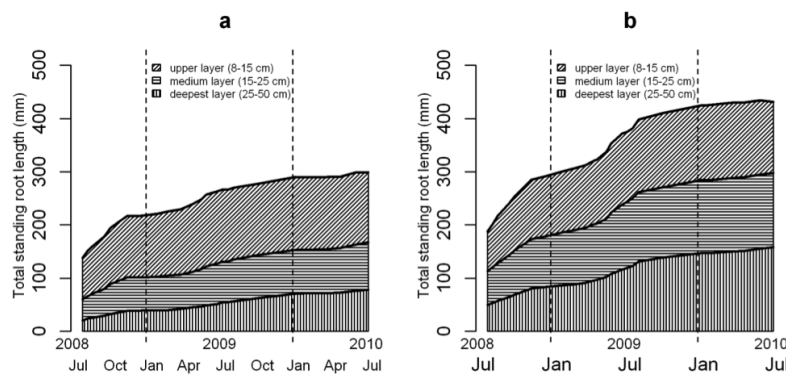


Figure 12: The left panel (a) displays the average root length in different parts of the soil for plots with ambient CO₂ (8-15 cm, 15-25 cm and 25-50 cm soil depth). The right panel (b) shows the average root length for plots with elevated level of CO₂. At the end of the study significantly longer root lengths were observed for the whole soil profile ($p=0.024$) and in each soil layer.

Herbivory

Defoliation impacts the plant directly via a reduction in photosynthetically active biomass and also affects consumers of plant products below ground. We performed defoliation of *Deschampsia* in spring and autumn and analysed the effects on soil biota as dependent on climate change.

One big question behind our work with plants in interaction with consumers of plant carbon is to what extent the plant is in charge. Which heterotrophs induce a response from the plant that can be regarded as a defence, and which heterotrophs can act on the plant

as if it was a sack of sugar water that you can puncture.

With the grass (*D. flexuosa*) we made two very similar studies that gave quite contrasting results. In the first (Stevnbak et al. 2012) we let the grasshopper (*Chorthippus brunneus*) feed on the plants in the very late season. In this case results indicated that defoliation induced the plant to release more organic carbon from the roots to the benefit of microbial growth (Figure 13). Moreover, we observed an increased cascading effect of herbivory below ground all the way to protozoa at elevated CO₂ (Figure 14b) as opposed to ambient CO₂ where the effect on soil biota was smaller (Figure 14a).

Convention will then suggest that the plant by this action acquires more nutrients for re-establishment after defoliation because the plant-induced increase in microbial activity will also release nutrients from soil borne sources to the benefit of the plant.

Redoing the defoliation study in the spring of 2011 - this time with scissors - there was absolutely no evidence for an increased root exudation as found in the previous study, rather the opposite. Soil nematodes were reduced in number following defoliation in the spring. At elevated CO₂ soil organisms were stimulated in accordance with the above-mentioned study from autumn(Figure 15).

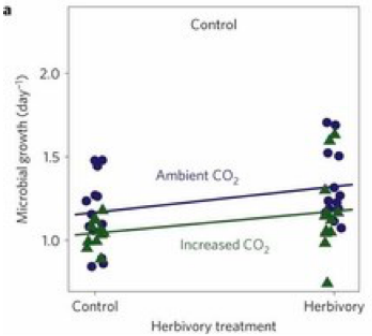


Figure 13: Limitation of microbial growth. Results from microbial growth assays on soil samples from plants grown with or without grasshopper herbivory and exposed to ambient CO₂ (circles) or increased CO₂ (triangles) and with addition of carbon (a). Aboveground herbivory increased below-ground microbial growth when only carbon was added (a; $P=0.02$). From Stevnbak et al. 2012

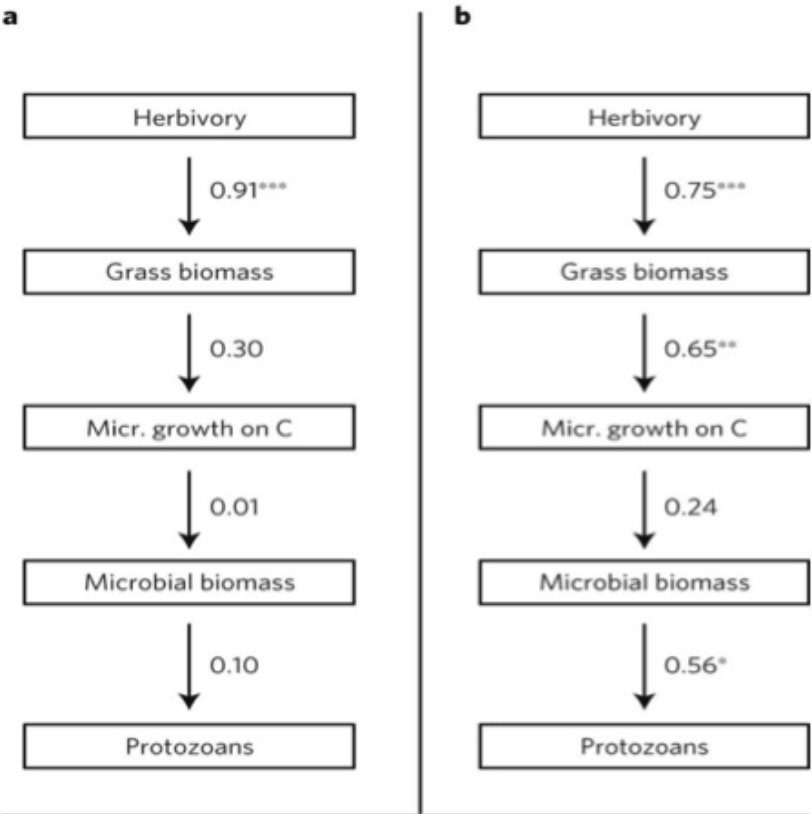


Figure 14: Effects of increased CO₂ on above-below-ground interactions. Shown are the pairwise correlations between individual variables, with significance indicated by asterisks (* $P<0.01$; ** $P<0.001$; *** $P<0.0001$). Corresponding structural equation models produced essentially similar results but are not included here because the number of replicates precludes the use of structural equation models in this case. a, ambient CO₂; b, increased CO₂. From Stevnbak et al., 2012.

When we compare the results of the autumn and the spring defoliation, plant shoots were growing in the spring study, and this growth was stimulated by defoliation whereas the plants did not grow following defoliation in the autumn study (data not shown).

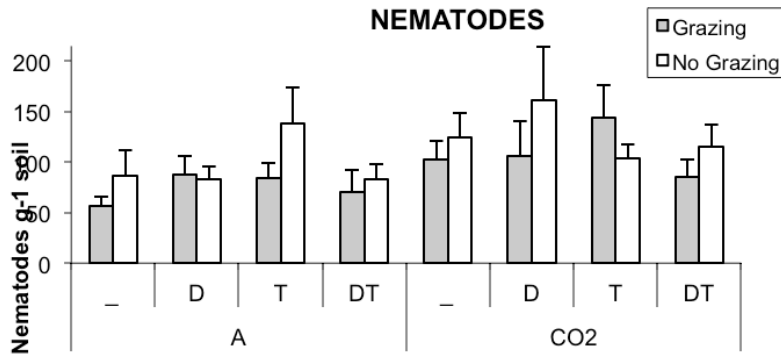


Figure 15: Soil nematode number after one month of defoliation of *D. flexuosa* in April 2011. From Marie Dam, unpublished.

We therefore have a problem with the conventional explanation of increased exudation in the autumn being a means for the plant to increase nutrient uptake from the soil when this does not occur in the spring where the plant certainly is in need of nutrients being in the active growing phase. So, taking the results of the two studies together the story probably is that plants are in charge when they grow actively, and avoid wasting photosynthesis products on soil heterotrophs. When active growth is over due to time of season, plants just release carbon when attacked because at that time there is no chance to recover anyhow.

Herbivores on the heather plant face larger changes to their growth conditions under global change than herbivores on grass. This is because heather (a dicotyledon) as opposed to grass (a monocotyledon) have secondary compounds in their leaves that affect herbivore performance and the production of these is affected by growing conditions such as CO₂, temperature and moisture. We studied this with larvae of the heather beetle left on the plants at Brandbjerg for five weeks. Larvae performed worse at any climate change. Larval weight as well as survivorship of the heather beetle (Figure 16) was reduced at any treatment, mostly by the drought. This clearly suggests that any combination of climate change will affect performance of the heather beetle negatively.

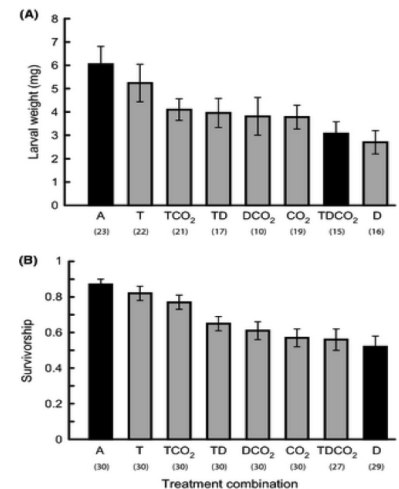


Figure 16: Effects of combinations of climate change treatments on (A) mean larval weight and (B) mean larval survival. Black bars indicate the two most extreme conditions applied in this experiment – either "fully ambient" or "full climate change", that is, a combination of all three climate change treatments. Sample sizes are given in brackets. From Scherber et al. 2013.

Impacts on soil organisms

Soil microbiology

In the uppermost 10 cm of the soil at Brandbjerg, each gram of soil harboured between 0.5 and 2 billion bacteria (Bergmark et al. in prep a), which is fairly low compared to other temperate soils that usually harbour between 1 and 10 billion bacteria per gram, likely due to the low pH of the soil. The number of bacteria and fungi decreased dramatically with soil depth, but the treatments did not affect the distribution of soil bacteria and fungi at soil depths down to 50 cm. The soil bacteria at Brandbjerg were dominated by three groups, Acidobacteria (which favour low pH), Proteobacteria and Actinobacteria, while the soil fungi are dominated by *Trichoderma* molds and other genera involved in degradation of organic matter, as well as *Rhizoscyphus* spp., *Oidiodendron* spp. and other genera associated with roots (Haugwitz et al., submitted a). Despite pronounced differences in soil organic matter content under the two dominating plants, with higher soil organic matter content under heather than wavy hairgrass (Nielsen et al. 2009), soil fungal abundance and diversity only showed small differences (Bergmark et al., in prep. a).

Interestingly, soil bacteria and soil fungi responded differently to the global change treatments (Haugwitz et al., submitted a). In general soil bacteria only showed minor responses to the treatments and the responses were mainly related to the warming treatment, which increased bacterial activity or abundance (Larsen et al. 2011, Andresen et al. 2014, Bergmark et al., in prep. b, Haugwitz et al. 2014). In contrast, we observed more responses of the soil fungi especially related to the drought treatment, which increased fungal activity or abundance (Haugwitz et al., submitted b) and to elevated CO₂ increasing e.g. arbuscular mycorrhizal colonization of grass roots (Arndal et al. 2013, Merrild et al., submitted). The increased colonization by arbuscular mycorrhiza may facilitate plant nutrient and water uptake and enhance soil carbon sequestration by the ecosystem under elevated CO₂.

While bacterial community structure remained the same during the year, the fungal abundance, community composition and functionality change and were altered differently by the global change manipulations depending on the season (Haugwitz et al., submitted a, Merrild et al. submitted). An extended growing season due to elevated temperature increased the relative abundance of free-living

fungi and decreased the relative abundance of root-associated fungi in November (Haugwitz et al., submitted a), while colonization of grass roots by arbuscular mycorrhiza was lowest in March (Merrild et al., in prep. a) but stable throughout the year in the future climate treatments combined.

During the early phase of the experiment, drought reduced decomposition of both heather and wavy hair-grass early phase litter (Andresen et al. 2010b). However, later in the experiment the drought treatment showed a stimulation of litter decomposition rates as well as CO₂ respiration and fungal abundance in litter placed in the plots several weeks after the drought treatment was terminated (Haugwitz et al., submitted b). We observed no distinct changes in fungal community composition in the litter in the drought plots, which suggested that the fungi were adapted to extended drought periods enabling them to be active at the often low water content associated with litter, or that they responded faster when conditions became favourable (Haugwitz et al., submitted b). This finding may have implications for our understanding of litter decomposition and thereby carbon loss from grass- and shrub-dominated ecosystems, many of which are likely to experience changes in future precipitation patterns.

The drought treatment also had a positive effect on N₂ fixation by bacteria living on mosses. Here, drought increased N₂ fixation rates and abundance of the *nifH* gene, a key gene involved in the N₂ fixation process (Dyrnum et al., submitted). In the drought treated plots, the distribution of *nifH* on mosses shifted towards the brown moss fraction, which was less prone to desiccation compared to the green moss fraction (Dyrnum et al., submitted). Warming also increased *nifH* abundance on the mosses, while in soil neither N₂ fixation rates nor *nifH* abundance was affected by the treatments (Dyrnum et al., submitted). We estimated the annual N input through N₂ fixation at Brandbjerg to be 101–139 mg N m⁻², corresponding to 11 % of total N deposition in the area (Dyrnum et al., submitted). This, combined with increased abundance of N₂-fixing bacteria due to drought and increased temperature, suggested that the N input to the ecosystem through N₂ fixation may increase in the future.

Global change affects plant communities in many globally important shrub- and grassland ecosystems, often leading to shifts between shrub and grass species. However, it is not known how these shifts in the dominating plant communities affect the response of soil fungal and bacterial communities to global change. Our experimental site provided a unique opportunity to test if global change affects soil micro-organisms differently under two contrasting plant species, wavy hair-grass versus the dwarf shrub heather. We found differences in the microbial communities under the two plant species, but only observed few and minor changes in the community composition due to the different global change factors, demonstrating a high robustness of the soil microbial communities under both plant species (Bergmark et al., in prep. a). This lead us to conclude that

vegetation shifts between the shrub and grass species induced by future global change may change soil microbial community composition, but these changes will not affect the overall response of soil microbial communities to global change. Overall, the observed treatment effects on soil bacteria and fungi affected the C and N pools and fluxes in the ecosystem (Andresen et al. 2010a; Larsen et al. 2011). The main drivers of changes to the soil bacteria and fungi were single-factor treatments, mainly elevated temperature increasing bacterial abundance and activity, and drought increasing fungal activity and abundance. However, the single-factor effects were generally extinguished by the multi-factor treatments resulting in little or no difference between the future climate scenario and the ambient control.

Responses of soil fauna

Pools

Soil dwelling (euedaphic) Collembola are less exposed to drought conditions and have efficient drought-protective physiological mechanisms to resist low water potential (Holmstrup and Bayley 2013), whereas surface dwelling species are more exposed, and therefore more vulnerable to long-term drought (Holmstrup et al. in preparation). We did not observe overall persistent declines of Collembola numbers due to the drought treatment, and it is unlikely that future increased drought will have any significant impact on these animals at our latitudes (Holmstrup et al. 2013). Soil mites have efficient water-conserving cuticles and are not negatively impacted by drought in any INCREASE³ or CLiMA!TE experiments. On the other hand, more soft-bodied species, like nematodes and enchytraeids, are extremely sensitive to low water potential and therefore clearly impacted by drought (Figure 17) (Maraldo et al. 2008, Maraldo et al. 2009, Maraldo and Holmstrup 2009, Maraldo et al. 2010, Andresen et al. 2011). However, enchytraeid populations recover within 2-4 months after re-wetting of the soil (Maraldo and Holmstrup 2009, Holmstrup et al. 2012), meaning that the ecosystem functions of enchytraeids are only transiently reduced or brought to a complete arrest during periods of extreme drought, and relatively quickly recovering thereafter (Maraldo et al. 2011, Holmstrup et al. 2012). The same conclusion applies to the abundance of nematodes (Dam et al. in preparation).

Warming did generally not affect mesofauna, e.g. no effects of warming were detected for enchytraeids, but sometimes we observed positive effects on micro-arthropods (Holmstrup et al. in preparation, Holmstrup et al. 2012, Holmstrup et al. 2013). Warming reduced all nematodes including the dominant trophic group, the root herbivores, by almost 50% in the upper layer. The remaining assemblage of root herbivorous nematodes, however, shifted towards species with longer generation times, possibly because of an earlier

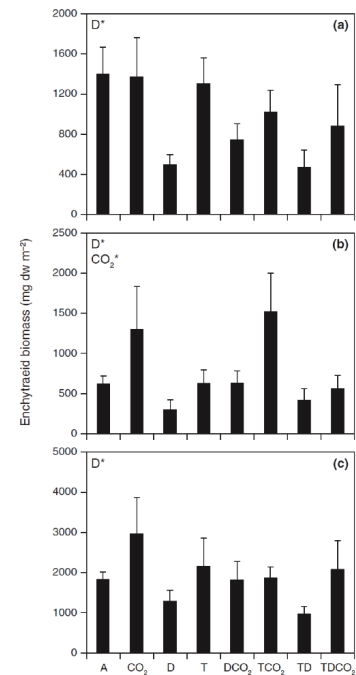


Figure 17: The biomass of enchytraeids was consistently reduced by drought, and at some samplings stimulated by CO₂. Columns indicate enchytraeid biomass (mg dry weight m⁻²) in samples collected from the 0–9 cm soil layer (N = 6, mean ± S.E.) in (a) autumn 2006, (b) summer 2007 and in (c) autumn 2007. Annotations show which effects were determined to be significant and the significance level (p < 0.05) is marked by an asterisk (*).

³ INCREASE is an EU-funded infrastructure of 7 large-scale climate change experiments and a phytotron designed to study climate change effects on shrublands.

start of plant growth and/or because of better survival of these nematodes (Stevnbak et al. 2012).

Increased atmospheric CO₂ is unlikely to have any direct effects on soil fauna since CO₂ in soil pore space is always orders of magnitude higher than in the atmosphere. Any effects on soil fauna attributable to increased CO₂ must therefore be of an indirect nature. In fact, we did observe significant effects of CO₂ for nematodes and enchytraeids, but generally not for micro-arthropods. Increased CO₂ stimulated long-lived and carnivorous/omnivorous nematodes, likely due to an increased root biomass and root exudation increasing the microbes and prey that this group of nematodes is feeding on. Enchytraeids and oribatid mites were stimulated by increased CO₂ in some periods, probably due to better provision of labile carbon resources (Maraldo et al. 2010, Andresen et al. 2011). Interestingly, we also observed that increased CO₂ counteracted the negative effects of drought on enchytraeids (Maraldo et al. 2010).

Soil fauna biodiversity

Although total enchytraeid abundance seemed not to be persistently affected by annually repeated drought, significant effects were detected for species richness and community structure. Thus, long-term experiments with repeated and intensified droughts caused a reduction of species richness, whereas warming or increased CO₂ did not have any effect. Species known to prefer moist or wet conditions were reduced or disappeared in the drought treatment.

Functions of soil fauna

The transient reductions caused by drought have the consequence that less N is mineralized by the soil fauna during these periods (Larsen et al. 2011). However, since the overall biomass of soil fauna is recovered relatively soon after re-wetting of the soil, such effects are probably not of great importance for the ecosystem processes mediated through soil fauna.



Figure 18: Collembola. ©Steve Hopkin.

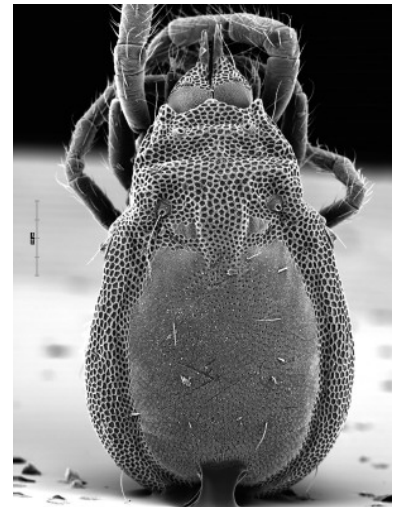


Figure 19: Oribatid mite. ©Josef Stary.



Figure 20: Enchytraeid. ©Karina V. Fisker.

Impacts on ecosystem functioning

Greenhouse gas fluxes

The exchange of non-CO₂ greenhouse gases between the heath-land and atmosphere was examined throughout one and a half year initiated nine months after the climatic treatments started. The site is a net-sink of methane (CH₄) at a magnitude comparable to other unmanaged ecosystems. Elevated temperature increased the CH₄ uptake by about 20%. However, during winter elevated CO₂ reduced the CH₄ uptake, which outweighed the positive effect of warming when analysed across the study period. Emissions of nitrous oxide (N₂O) were generally low, typically for unmanaged systems. The single climatic parameters had no major effect on the N₂O fluxes, but the combination of CO₂ and warming stimulated N₂O emission, whereas the N₂O emission ceased when CO₂ was combined with drought. The N₂O flux under the simulated future conditions was not different from the ambient control treatment. Overall, the study suggests that in the future, CH₄ uptake may increase slightly, while N₂O emission will remain unchanged in temperate ecosystems on well-aerated soils (Carter et al., 2011). Climatic feedbacks in terms of greenhouse gas emissions will thus stay neutral. Low abundance and activity of the N₂O-reducing enzyme nitrous oxide reductase suggests (Larsen et al., 2011; Bergmark et al., in prep.) that the cumulated N₂O emissions may convert into total N-gas losses from the ecosystem, thus indicating very low losses by this pathway, and unaffected by climatic changes.

Nitrogen cycling

The N cycle at the experimental site is characterized by a much higher flux of N within the system than arrives in bulk N deposition and N₂ fixation or leaves via leaching and N-gas production as generally seen in natural and semi-natural ecosystems (Larsen et al., 2011). Within the first two years, warming alone increased the internal N cycle, whereas drought had the opposite effect, and increased CO₂ had no effect (Larsen et al., 2011). After prolonged exposure to the climatic treatments, i.e. five years after initiation, we show that warming increased both gross N mineralization and gross nitrification rates. In contrast, gross nitrification was decreased by elevated CO₂, an effect that was more pronounced when elevated CO₂ was

combined with warming and drought. Moreover, there was an interactive effect between the warming and CO₂ treatment, especially for N mineralization: rates increased at warming alone but decreased at warming combined with elevated CO₂. In the full treatment combination, simulating the predicted climate, gross N transformations were only moderately affected compared to control, suggesting a minor alteration of the N cycle due to climate change (Björnsne et al., 2014).

Leaching of nitrogen was generally low, less than $1 \text{ g N m}^{-2} \text{ yr}^{-1}$, and was unaffected by the climatic perturbations within the first and second year (Larsen et al., 2011). This pattern seems to be persistent over the long term (Larsen et al. in prep.).

Soil respiration

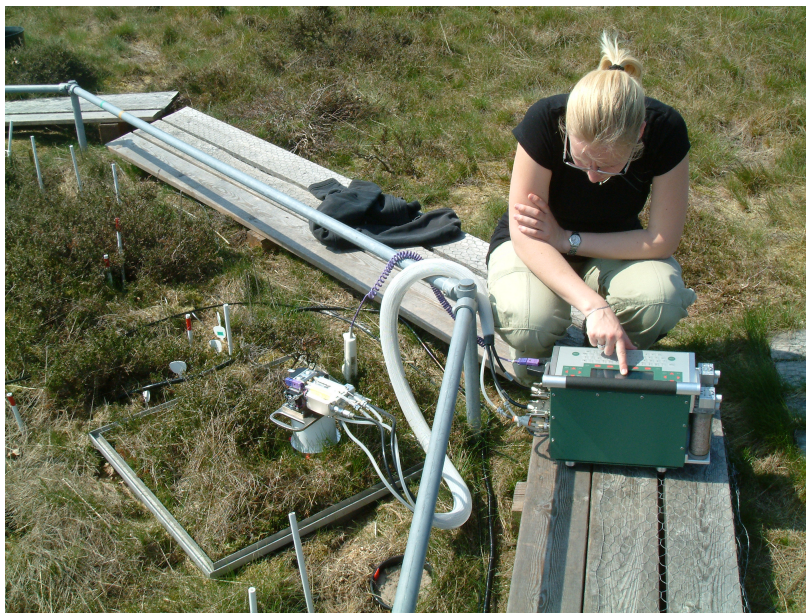


Figure 21: Set-up for measurement of soil respiration by vegetation free chamber. ©Inger Kappel Schmidt.

The average soil respiration, i.e. a measure of the total biological activity in the soil, increased rapidly in response to elevated CO₂ and a 38% increased activity could be observed over the three first years of measurements (Selsted et al., 2011; 2012). This increase was independent of combination with drought or increased temperature. In contrast, extended summer drought decreased soil respiration by 14%, and the activity was further reduced when summer drought occurred in combination with elevated temperature why this treatment alone did not affect soil respiration overall. A model extrapolation predicts that soil respiratory C losses would increase by ca 21% under the future climatic conditions. Therefore, in the future climate, stimulation of C storage in plant biomass and litter must be in excess of 21% for this ecosystem to not suffer a reduction in net ecosystem exchange (Selsted et al., 2012). Recent observations on soil respiration indicate that these responses patterns were persistent even after

seven years of treatments (Larsen et al., in prep). The increased respiration under elevated CO₂ concurred with separate observations that elevated CO₂ may stimulate not only soil microbial activity, but particularly induce sequential decomposition of soil organic carbon compounds, the so-called priming (Reinsch et al., 2013). In contrast, exposure to the full climatic combination did not induce priming (Reinsch et al., 2013).

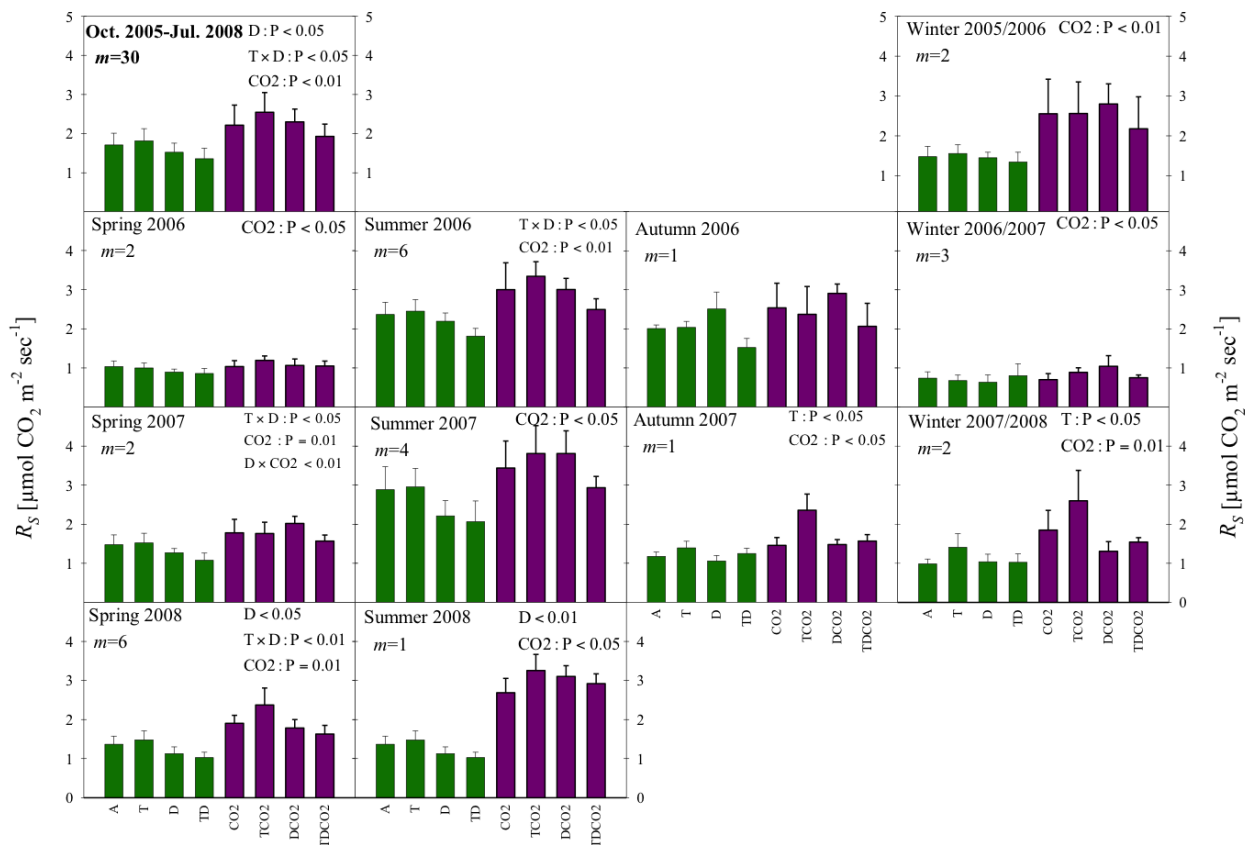


Figure 22: Soil respiration in different seasons during 2005–2008. Treatments at ambient CO₂ indicated in green and treatments with elevated CO₂ indicated in purple (From Selsted et al., 2012)

The turnover and utilization of labile carbon compounds in the soil root zone was mainly controlled by bacteria. The proportion of carbon turnover through fungi and actinomycetes was greater in the bulk soil. The utilization of recently assimilated C by the microbial community was faster under elevated CO₂ conditions and under the future climatic conditions, compared to ambient. In contrast, the utilization of recently assimilated C by rhizosphere associated actinomycetes was always lower under future climatic conditions (average 2%) compared to any other single- or two-factor treatment. We conclude that changing climatic conditions will affect C utilization by the soil microbial community (Reinsch et al., 2013; 2014).

Soil organic carbon

The pool of soil organic carbon (SOC) in the Brandbjerg heath-land constitute a significant 7745 g C m^{-2} (0-90 cm depth), which exceeds the amount of plant-bound carbon 15-fold (Arndal et al., 2013, Kongstad et al., 2012). The SOC is concentrated in the upper soil layers, and 35% is located in the top 0-10 cm soil depth. The majority 97% of the top SOC can be characterized as recalcitrant carbon associated to mineral particles with a relatively long 100-150 yrs mean residence time (MRT); ca. 1.5% SOC is characterized as labile low-density SOC with a MRT of 20-40 yrs, and ca. 1.5% as "occluded" SOC with intermediate MRT of 50-60 yrs (Thaysen et al., unpublished). In accordance with the SOC-pool characteristics effects of the climatic perturbations could mainly be observed in the small labile fractions. Both elevated temperature and CO_2 acted to decrease the stock of labile SOC (Thaysen et al., unpublished). Moreover, the major pool of slowly decomposable SOC decreased in the top soil when the temperature increased, whereas bulk analysis of SOC revealed an increase under conditions with extended drought periods. Meanwhile, when the three global change factors were applied in combination, the total SOC pool in the top soil remained unchanged during the experimental eight years course.



Figure 23: Soil profile at Brandbjerg.
©Rasmus Dalhoff Andersen



Figure 24: Octagons without and with extended curtains for demonstration purposes. ©Kim Pilegaard.

Ecosystem syntheses

Synthesis of the effects of climate change on ecosystem nitrogen turnover

Plant growth in most terrestrial ecosystems of the world is limited by nitrogen (N) and characterized by strong competition for N between plants and the soil communities of fungi and bacteria (Marion et al., 1989; Jonasson et al., 1996). Consequently, ecosystem N availability is an important factor controlling the carbon (C) uptake in terrestrial ecosystems and therefore also plays a dominant role in controlling the feedback between the biosphere and the atmosphere in a warmer and more CO₂-enriched world. The theory of N as a limiting factor constraining the C uptake in terrestrial ecosystems in response to elevated CO₂ is conceptualized in the Progressive Nitrogen Limitation (PNL) framework (Luo et al., 2004) describing how increased C sequestration driven by elevated CO₂ requires increased access to N in order to balance the C input. Accordingly, without additional input of plant-available N, nitrogen will progressively limit further C uptake. Most of the experimental evidence of PNL and the role of N in constraining C uptake is based on modelling studies (Rastetter et al., 1997) or on experiments involving elevated CO₂ alone or combinations with various levels of N addition to demonstrate the role of N in stimulating CO₂ sequestration responses (Lutze & Gifford, 2000; Lutze et al., 2000; van Heerwaarden et al., 2005; de Graaff et al., 2006; Reich et al., 2006). However, in a future CO₂-enriched world the N limitation and the CO₂ response in N-limited systems will to a large extent be regulated by the other climate change drivers, such as warming and changes in precipitation regimes, and these responses are not captured in experiments with elevated CO₂ alone. Since future climate change will involve simultaneous changes in all of these factors, it is important to understand the possible interactions between different climate drivers on N availability and limitation.

In the CLiMA!TE experiment, we synthesized the data on nitrogen cycling obtained during the first two years of treatments in the publication by Larsen et al. (2011). A total of 47 different variables had been measured during the first two years of the experiment including various pools of N (plants, litter, microbes, soil and soil fauna), N₂O emissions, potential nitrification and de-nitrification, atmospheric deposition, and N leaching. The combined analysis of the data revealed an ecosystem generally dominated by internal N

turnover compared to gains from atmospheric input and losses by leaching, and also showed the importance of the soil fauna for facilitating the internal N turnover (Figure 25).

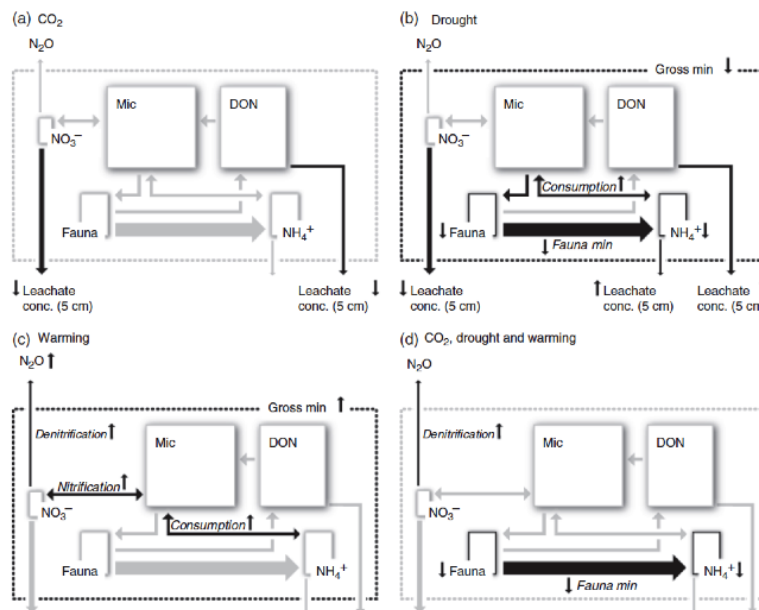


Figure 25: Pools (in bold, g N m^{-2}) and fluxes (in italic, $\text{g N m}^{-2} \text{y}^{-1}$) of N in ambient plots down to 10 cm soil depth (leaching below 60 cm depth) in 2007. See Larsen et al. (2011) for further details.

In response to elevated CO₂, we observed decreased leaf N content and increased leaf C/N ratios under elevated CO₂ for both dominant species, *C. vulgaris* and *D. flexuosa*, which concurred with down-regulated photosynthetic capacity (Albert 2011a). However, the increased C/N ratios observed in leaves after 2 years of treatments were not large enough to affect whole plant biomass C/N ratios. The below-ground N turnover was reduced by drought and increased by warming while direct effects of elevated CO₂ were minimal (Figure 26). However, with all three factors combined the reduction of N turnover caused by drought prevailed although with decreased intensity (Figure 26).

Synthesis of the effects of climate change on ecosystem carbon balance

Net ecosystem CO₂ exchange (NEE) and ecosystem respiration (RE) were measured intensively during campaigns in 2011 and 2012 and the difference ($\text{NEE} - \text{RE} = \text{Gross ecosystem photosynthesis (GEP)}$) was estimated. Preliminary data analysis (Larsen et al., in prep) shows that the ecosystem was a sink for carbon and indicate that long-term exposure of the ecosystem to each of the climate change factors alone led to further increase of the net C uptake (Figure 27). In contrast, exposure to the full combination with all climate change factors simultaneously reduced the net C uptake by more than 50%. This demonstrates important interactive effects among the climate change factors with major implications for ecosystem C feedback

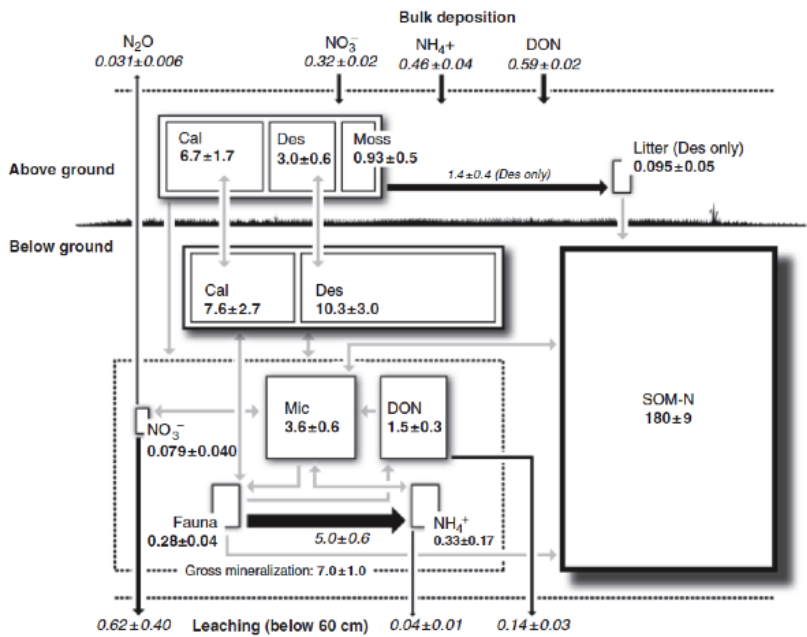


Figure 26: Below ground changes in N pools, N fluxes/processes and N concentrations caused by single treatments factors (a–c) and when all treatments are combined (d). See Larsen et al. (2011) for further details.

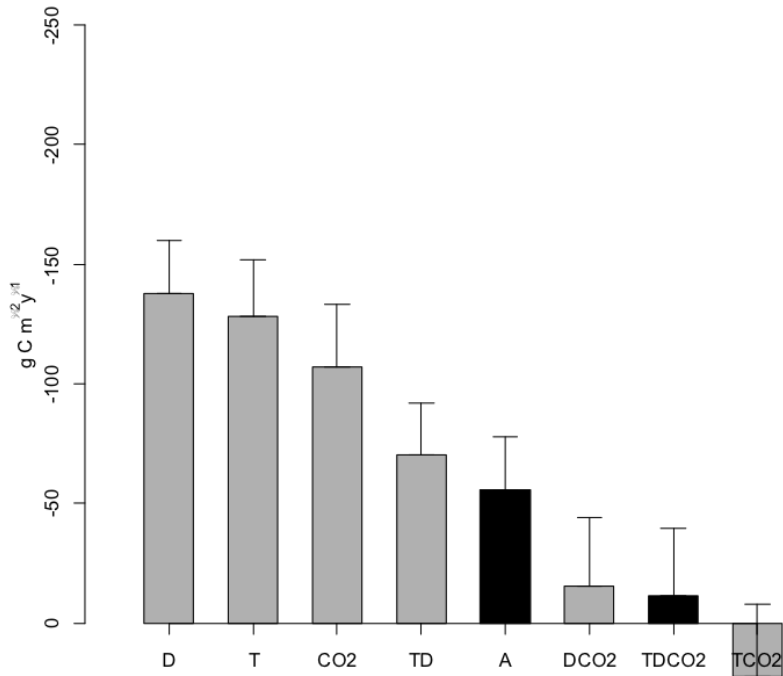


Figure 27: Preliminary data (ranked) of net ecosystem carbon exchange in 2011 across treatments. Negative values indicate ecosystem carbon uptake. Larsen et al. (in prep.)

under future climate. The results further indicate that reduction in net C uptake occurred in all combinations with elevated CO₂ because soil respiration was persistently stimulated more than photosynthetic assimilation in the treatment combinations (not shown). Coupled interactions are currently not very well reflected in existing Earth System Models causing potential over-prediction of future ecosystem carbon storage (Leuzinger et al. 2011). The results may therefore be highly valuable for testing and improving projective climate C-cycle models, which currently depend on response functions primarily derived from long-term observations under current climate or from single-factor climate experiments.

Interactions

In addition to the general understanding of responses of specific processes, compartments, or the whole ecosystem to the different treatments alone and in combination, CLiMA!TE has clearly demonstrated that interactions among the climate change factors do occur at all levels in the ecosystem and that these may not be easily predicted from the single factor responses. On the other hand, the results also demonstrate that most of the interactions are antagonistic leading to a reduction in the responses as opposed to the expectation when looking at the individual responses (Larsen et al., 2010). Especially when CO₂ is combined with higher temperature and/or drought, we observed that the magnitude of the effects became smaller than anticipated (Larsen et al. 2010), which agrees with early indications from the Jasper Ridge experiment in California (Shaw et al., 2002). These findings contribute to and support syntheses of results across many experiments and observations that increasing scale (size, time and number of impact factors) seems to reduce the magnitude of effects (Leuzinger et al., 2010; Dielemans et al., 2012). Our experimental findings indicate that "amplifying runaway processes" are not the norm and that long term multi-factor experiments like CLiMA!TE provide crucial knowledge for process understanding as well as model validation.

In fact, a general trend across the 47 measured N-related variables was a significant amount of interactions between climate drivers, the majority of which were antagonistic, i.e. effects observed in single factor treatments were reduced in treatment combinations (Figure 28) indicating that the ecosystem seems more robust to climate change when these factors are imposed in combinations. Still, the observed negative response to drought of soil fauna biomass and N mineralization and *D. flexuosa* litter N production prevailed in the full treatment combination and so did the increased leaf C/N ratios of the dominant species *C. vulgaris* and *D. flexuosa*. If persistent, these changes are likely to lead to reduced N availability and possibly to progressive N limitation under elevated CO₂ in the experiment.

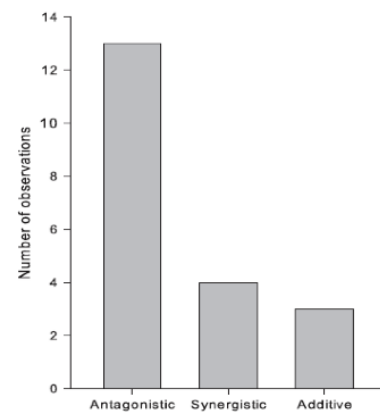


Figure 28: Observed significant interactions were categorized as antagonistic, i.e. treatment combination lead to reduction of effects, or as synergistic, i.e. combination lead to amplification of single effects or significant effect was only observed in combination. Number of observed simple additive effects is also shown. See Larsen et al. (2011) for further details.

Perspectives

CLiMA!TE and extreme events

CLiMA!TE was initiated in 2004 and after a pretreatment year, the manipulations of CO₂, temperature and precipitation were applied from autumn 2005 and carried out for more than 8 years to 2014. Scenarios that were chosen for the treatments have not changed very much since then. The atmospheric CO₂ concentration has continued to rise (increased by ca 20 ppm during the course of the experiment) and our choice of 510 ppm would most likely also be a reasonable choice today. Similarly, the temperature scenario of ca 2°C increase is still a valid prediction although probably at the lower end of what is expected today – and in addition our experimental approach only allowed a 1°C increase. Finally, the precipitation scenario with a ca 4 weeks summer drought is also a likely frequent scenario for the future. So, the scenarios chosen for CLiMA!TE 10 years ago would probably still today be likely candidates for treatments if a new experiment was to be initiated. However, our understanding of the complexity and dynamics of weather extremes have developed significantly over that decade from being what may appear as an unreflected more frequent and more severe "single events" based idea to being understood as a very fundamental but unpredictable and complex event or series of events. We know that weather patterns will (and already have) lead to more variable weather patterns with bigger fluctuations in both temperature and especially precipitation and that for example the increased variability in precipitation patterns with less frequent but larger rain events will have impacts on ecosystems at all moisture regimes (dry, mesic and wet) (Knapp et al, 2008). We also know that future weather patterns will most likely be characterized by more frequent "extremes" and that these extremes will be more extreme than in the past (IPCC 2014). We also know that while many of these extremes will be within the range of extremes that the ecosystems already have experienced and may be adapted to, they will occur more frequently which we have shown may lead to new and hitherto unknown long term effects (Sowerby et al., 2008). However, future extremes in both temperature and precipitation will also go outside the range of currently observed extremes and the general understanding including experiences from CLiMA!TE call for a new generation of experiments (Beier et al., 2012; Kreyling and Beier, 2013; Kayler et al., 2013). As mentioned above, CLiMA!TE applied a

relatively moderate drought because of the long term perspective of the experiment. We did not want to disturb the ecosystem severely as this might confound the long-term perspective. This has two consequences that constraints the knowledge generated and calls for a new generation of experiments:

1. The ecosystem generally appeared robust to the treatments applied in CLiMA!TE (effects were relatively moderate) which in itself may be a consequence of the moderate treatments causing a relatively small signal-to-noise ratio. More extreme (but still likely/realistic) treatments might have caused larger effects.
2. The "extremes" were purposely kept moderate in order not to be too harmful or disturbing. However, one of the most interesting characteristics of the future climate and the associated extremes is that they may lead to exceedance of tipping points and critical thresholds for single processes or whole ecosystems. The apparent resilience of the CLiMA!TE ecosystem may be a consequence of the fact that the system was never pushed out of its stable state. We know from disturbance ecology that major disturbances may lead to ecosystem transitions and future extremes may in fact act like disturbances and lead to major changes and transitions in ecosystem structure and functioning. The CLiMA!TE experiment, and most other experiments with it, does not provide much insight into such changes.

CLiMA!TE - directions for future experiments

As a consequence of the experimental design of CLiMA!TE and most other climate change experiments conducted in the past and still it has to be realized that our "experimental window" is limited. There is no doubt that the experimental design of CLiMA!TE was reasonable and with minor modifications would be a likely design to be chosen if a new experiment would be started today. However, it also means that our results do not inform sufficiently about some of the potentially most relevant and decisive situations in the future - the situations that may cause significant shifts in ecosystem behaviour

The example mentioned earlier with regeneration of the *C. vulgaris* after an outbreak of heather beetles showed that even moderate changes in climate may have large impact on plant communities if applied to ecosystems after a severe disturbance. We therefore need a new generation of experiments focusing on tipping points, disturbances, mortality and recovery (Beier et al., 2012; Kreyling and Beier, 2013; Kreyling et al., 2013; de Boeck et al., 2015; Kayler et al., 2015). Such a design is on the other hand not easy to come up with.

While the CO₂ scenario is very easy generally proposing one level of CO₂ which will be globally true and acceptable, the complexity in extreme events scenarios is massive. For example extreme precipitation events can involve a combination of both long lasting droughts and severe flooding events which can occur at different times of the

season and various frequencies and at various intensities. For precipitation this means that it will be impossible to define one "realistic scenario" (as is the case for CO₂). The factors can be combined to thousands of scenarios being equally relevant and realistic - and the one we choose is unlikely to ever happen. In extreme events, the generally applied idea in ecosystem experiments of applying "realistic scenarios" is therefore not very feasible. New approaches are needed.

We propose two necessary avenues:

1. Gradient studies/Regression design - The choice in CLiMA!TE of applying each of the three factors at one level and in sufficient replicates to gain statistical power is a common and overwhelmingly used approach and has the advantage that it is well known by reviewers and that results can be analysed with commonly used statistical models. However, it also has the significant limitation that we only know the response to that one level of the treatment which was applied. For CO₂ this is probably a minor problem since the future atmospheric CO₂ concentration is relatively well predicted and will not be subject to large fluctuations or local differences. But, for temperature and especially for precipitation the predicted future level of these are subject to much larger uncertainty and regional variations. Hence, in the context of extreme events where we want to know the critical thresholds and tipping points the knowledge of the response to one given level of temperature or water is of little value. We would much rather like to know the responses at different intensities of the factor ranging from modest changes to levels even exceeding the threshold. We want to move from response points to response surfaces. There are statistical methods available to handle such designs using regression statistics instead of classic ANOVA where all the different levels of a given factor become part of the replication. This may sound simple, but when we at the same time want to combine three different factors it obviously becomes (Kreyling and Beier, 2013). Combining 3 factors at for example 5 different levels in all potential combinations would require many experimental units and will not be feasible in most cases, and deliberate selections of treatment combinations within the possible range would be needed. However, if done carefully, such a regression design could clearly lead to a much stronger level of information about process responses which would also increase the information of ecosystem models.
2. Combined process experiments and modelling – Another complementary approach would be to conduct experiments focused on threshold exceedance and combine these with models (Beier et al., 2012; Kayler et al., 2015). The models cannot model critical thresholds and the consequences of exceeding tipping points unless the necessary biological process understanding exists and is included in the models. However, this is often not the case today. We often

do not know what level of drought will kill plants and how the recovery proceeds afterwards under a range of conditions. Therefore we need to understand these processes and conceptualize this in models. This is further important because with the vast amount of potential future scenarios it is impossible to test them all experimentally. We therefore need some basic understanding of process and ecosystem responses to various climate change factors alone and in combination embedded in models which can then be used to make ranges of predictions.



Figure 29: Sunset at Brandbjerg.
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Figure 30: Project members playing with the alphabet in the grass.
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Appendix: Publications from the CLiMA!TE project

Scientific publications

1. Beier, C. (2004) Interactions of elevated CO₂ and temperature on terrestrial ecosystem structure and functioning – the role of whole-ecosystem manipulation experiments. *New Phytologist*, 162, 243-245.
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Aerial photography of CLiMA!TE experimental site with both rain and warming curtains extended for demonstration purposes. ©Kim Pilegaard.